

HOME-RANGE SIZE AND USE OF SPACE BY ADULT MOHAVE GROUND SQUIRRELS, *SPERMOPHILUS MOHAVENSIS*

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Using radiotelemetry we studied home range and movements of 32 adult female and 16 adult male Mohave ground squirrels (*Spermophilus mohavensis*) in the western Mojave Desert of California during 1990 and from 1994 to 1997. In 3 of the 5 years of study (1990, 1994, and 1996), early winter precipitation (October–January) was <30 mm, and no reproduction occurred at the study site. Postmating home ranges of females varied considerably among years, with annual medians for minimum convex polygons ranging from 0.29 to 1.90 ha. Females used the largest home ranges both during years of ample rainfall and reproduction (1995 and 1997) and during the year of most extreme drought and no reproduction (1990). We hypothesize that variation in home-range size among drought years may result from varying levels of food availability. In 1997, we also studied movements of adults during the mating season, from mid-February to mid-March. During this period, adult males made extensive movements, resulting in median minimum convex polygons much larger (6.73 ha) than those of females (0.74 ha). Such movements would have made it possible for males to locate adult females soon after their emergence from hibernation. Patterns of variation in home-range size and movements observed during this study may reflect adaptive responses of this small herbivore to a highly variable, arid environment.

Key words: home range, Mohave ground squirrel, Mojave Desert, movements, productivity, radiotelemetry, *Spermophilus mohavensis*

The size of an animal's home range may reflect its resource needs, distribution and abundance of resources, or population density. McNab (1963) showed that home-range size varies among mammal species as a function of body mass and trophic level. Harestad and Bunnell (1979) argued that differences in habitat productivity (e.g., between seasons or years) should affect home-range size: as habitat productivity increases, a smaller area is required to meet resource needs, resulting in a smaller home range. Food supplementation experiments (reviewed by Boutin 1990) have shown the expected inverse relationship between increased food availability and decreased home range for a variety of vertebrates, including reptiles, birds, and mammals. However, increased intruder pressure, attraction of competing species to supplemental food, or clumped distribution of resources may lead to results differing from the predicted inverse relationship (Kodric-Brown and Brown 1978; McShea and Schwede 1993; Slade et al. 1997). Studies exam-

ining the relationship between seasonal variation in resource availability (Beier and McCullough 1990; Bobek 1977; Singer et al. 1981) or spatial variation in resource abundance (Relyea et al. 2000) and home range are less common.

The Mohave ground squirrel (*Spermophilus mohavensis*) is found only in the western Mojave Desert of California, where it occurs in desert scrub habitats, usually on flat to gently sloping terrain with alluvial soils (Best 1995). Because of habitat loss and fragmentation, it currently is listed as threatened under the California Endangered Species Act. Mohave ground squirrels, like other mammals in arid environments, must survive and reproduce not only when habitat productivity is very low and highly seasonal but also when it varies greatly from year to year. Therefore, home-range size and use of space by Mohave ground squirrels might change in response to annual variations in resource availability.

Foliage and seeds of native shrubs and forbs make up most of the Mohave ground squirrel's diet. During the mating season, shrub foliage is the most important dietary component (Best 1995). In years with sufficient winter rainfall, forbs dominate the diet during the subsequent late spring and early summer. During drought years, production of forbs is much reduced, and shrub foliage remains the predominant food resource throughout the active period. Winter drought makes it particularly difficult for

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adult females to meet energy demands of reproduction and then accumulate fat reserves needed for dormancy. In years with low winter rainfall, female Mohave ground squirrels do not produce offspring and may enter hibernation as early as the end of April.

We predicted that adult home-range size in this species should decrease in years of high winter rainfall and habitat productivity, increasing in size when rainfall and productivity are low, in accordance with the habitat-productivity hypothesis. Size of home ranges of adult female should increase during reproductive years because of energy requirements of reproduction. Home ranges of adult males should be larger in the mating season to increase access to receptive females (Dobson 1984; Schwagmeyer 1988).

We studied postmating home range and movements of adult Mohave ground squirrels in 1990 and from 1994 through 1997 and movements during the mating season in 1997. In 3 of these years, winter rainfall and primary productivity were low, and we observed no evidence of production of young. In the 2 other years, winter rainfall and food production were sufficient to support recruitment of young. Thus, this 5-year study allowed us to assess home-range size and movements relative to considerable variation in habitat productivity and in energy requirements of reproductive females.

MATERIALS AND METHODS

Study site and subjects.—Mohave ground squirrels are small (100–150 g adult posthibernation mass) diurnal rodents that are usually active aboveground from February through July but spend the rest of the year in dormancy (Bartholomew and Hudson 1960). The single annual mating season occurs immediately after emergence from hibernation in February and early March (Best 1995). Young are usually born in late March and early April, and lactation continues through mid-May (Pengelley 1966). Litters generally appear aboveground in early to mid-May.

We conducted our study in the northwestern Mojave Desert, Inyo County, California (36°04'N, 117°48'W). The 47-ha study site was a small valley within the rugged uplands of the Coso Range, a desert mountain range about 20 km east of the Sierra Nevada. Elevation of the study site was 1,400–1,500 m, and slopes ranged from 2–15%. Deep alluvial soils were classified as loamy coarse sands. Vegetation was a mixed desert scrub community. Important shrub species included spiny hopsage (*Grayia spinosa*), fourwing saltbush (*Atriplex canescens*), shadscale (*A. confertifolia*), cheesebush (*Hymenoclea salsola*), Cooper's boxthorn (*Lycium cooperi*), and winterfat (*Krascheninnikovia lanata*). This community is typical of the transition between Mojave and Great Basin desert biomes (Beatley 1975). Mean annual precipitation (1949–1999) was 163 mm at Haiwee Power Plant (elevation 1,160 m), 15 km to the northwest of the study site. Winter rainfall predominated, with 79% of annual precipitation received between 1 October and 31 March during the 51-year period of record. Primary productivity in the western Mojave Desert occurs mainly from March through May and is closely related to winter rainfall (Beatley 1974), which is highly variable from year to year. We maintained a rain gauge on the study site and collected precipitation data monthly.

A 22-ha portion of the study site, with trap stations placed at 50-m intervals, was used exclusively for radiotelemetry studies in 1990 and 1994–1997. The remaining 25-ha portion of the site, with trap stations at 25-m intervals, was used primarily for demographic studies from

1988 to 1996. We also carried out radiotelemetry in this portion of the study area in 1990 and 1997.

Capture procedures.—Ground squirrels were captured with Pymatuning (10 × 11 × 39 cm, Warren Grieser, Pymatuning, Pennsylvania) or Sherman (8 × 9 × 30 cm, H. B. Sherman, Tallahassee, Florida) traps placed under shrubs at each trap station and baited with commercial horse feed composed of corn, oats, barley, and molasses. Traps were set in early morning, checked at midday and late afternoon, and then closed for the night. Weight, sex, age, and reproductive condition were recorded for all captured ground squirrels. We marked ground squirrels for permanent identification with passive integrated transponder tags implanted subcutaneously between the scapulae with a hypodermic needle. Adults could be distinguished from juveniles by body mass and pelage. Adults that had been captured and marked previously as juveniles could be assigned to a specific age class. Reproductive condition of adult males was based on position of the testes (abdominal or scrotal). Adult females were examined for swelling of the vulva and nipple size and condition and palpated for evidence of pregnancy. They were then categorized as nonreproductive, receptive, pregnant, lactating, or postlactating.

Radiotracking.—We equipped 56 adult ground squirrels (36 females and 20 males) with radiotransmitters (Model SM-1, AVM Instrument Co., Livermore, California) mounted on flexible collars. The numbers of each sex equipped with radiocollars reflected the sex ratio of captured animals. Six adult females were radiocollared during more than 1 year of study, including 2 individuals that were studied during 4 consecutive years. Radiocollars weighed 5 g and were less than 5% of adult body mass. We located radiocollared individuals during daylight hours using portable receivers (AVM Instrument Co.) and handheld, 2-element Yagi antennas (Telonics Inc., Mesa, Arizona). We followed radio signals on foot until a ground squirrel was either seen or located underground to within 5 m by signal strength and direction. Locations were recorded using compass bearing and distance from the nearest trap station.

We attempted to recapture radiocollared animals at various times to collect data on mass and reproductive condition before their emergence into hibernation. This allowed us to monitor their condition and examine the fit of radiocollars. We attempted to retrieve radiocollars after emergence from hibernation the following spring by trapping in the vicinity of known hibernation locations. Although no radios were transmitting after this time interval, we recovered 39% of radios by this method.

Radiotracking was conducted periodically during the active season (February–July). For analysis, we divided radiotelemetry data into 2 categories: mating season, the period between emergence from dormancy in February through 15 March, and postmating season, the period from 16 March through 30 June. The end of the mating season was established by working backward from the emergence of young from their natal burrows, using data on gestation and development of young (Pengelley 1966). We collected data from the postmating period in all 5 years of the study and from the mating season in 1997. Adults generally were trapped and equipped with radiocollars during an intensive sampling period in late March and early April. During this period, we attempted to locate each animal 2–3 times daily (morning, midday, and evening if possible). Another period of intensive radiotracking occurred from mid-May to mid-June. Between these intensive sampling periods, we made shorter visits to the study area, during which we typically located animals 1–2 times daily over a 1–3-day period. Radiotelemetry studies continued until animals entered hibernation, the timing of which varied considerably among years. The study was expanded in 1997 by adding intensive sampling during the mating season. Seven males and 6 females were equipped with radio

transmitters beginning on 14 February. During the 1997 mating season, we usually obtained locations for each individual 1–3 times per day.

Data analysis and home-range estimation.—Home-range size was estimated for adult Mohave ground squirrels by using all map locations derived both from radiotelemetry and live-trap captures. We calculated postmating home ranges for those adult Mohave ground squirrels for which we had ≥ 12 locations and radiotelemetry data in ≥ 3 weeks. Forty-eight Mohave ground squirrels (32 females and 16 males) met our criteria for calculating home ranges. The mean number of locations per individual was $27.1 (\pm 11.5 \text{ SD})$. We found no relationship between number of locations and postmating 100% minimum convex polygons (MCP—White and Garrott 1990; $r^2 = 0.005$, $P = 0.628$). To compare postmating home ranges among years, we eliminated records from before 16 March and after 30 June. Home ranges for the mating season of 1997 were calculated for 13 Mohave ground squirrels (7 males and 6 females) for which there were ≥ 10 locations. The mean number of locations per individual was $30.6 (\pm 12.9)$. We found no relationship between number of locations and mating season MCP for either males ($r^2 = 0.009$, $P = 0.837$) or females ($r^2 = 0.417$, $P = 0.144$).

The mean time difference between locations, for those locations that fell on the same day, was 234 min (± 59 min, $n = 1,213$) for the postmating period and 214 min (± 18 min, $n = 385$) for the mating season of 1997. We excluded the few locations that were determined < 2 h apart. These resulted from having checked the location of an animal more than once during a sampling period. White and Garrott (1990) suggest that locations could be considered independent if the time interval were sufficient for the animal to traverse its home range. Maximum observed rates of travel were lowest for females in the postmating season (maximum of 260 m/h) and highest for males in the mating season (maximum of 1 km/h). These rates of travel were such that animals were capable of traversing their home ranges within a 2-h period.

Location data for radiocollared Mohave ground squirrels were plotted on maps of the study area, and home-range size was calculated with the software program CALHOME (Kie et al., 1996). Two estimates of home range were made for each individual: the 100% MCP and the 95% adaptive kernel. Because no males were radiocollared in 1995 and only 1 in 1994, males and females were analyzed separately for differences among years. Differences were tested initially using Kruskal–Wallis 1-way nonparametric analysis of variance, followed by Dunn's test for multiple pairwise comparisons (Zar 1984) when the analysis of variance indicated significant variation among years. We compared sexes within years using the Mann–Whitney U -test and between seasons in 1997 using paired Wilcoxon rank-sign tests. The 100% MCP has the advantage of simplicity and long historical use in the literature. However, it includes unused space, gives no indication of relative intensity of use, and is very sensitive to small sample size and extreme outlying locations (White and Garrott 1990; Worton 1987). Kernel methods use a sample of locations to create a probability density estimate that may be interpreted as a utilization distribution (Van Winkle 1975; Worton 1989, 1995) and is not dependent on parametric assumptions. The bandwidth, a smoothing parameter, was selected by the least squares cross-validation method (Worton 1995).

Unusually long movements by adult males were observed during the 1997 mating season. Therefore, in addition to comparing home-range sizes between seasons, we compared movement distances of males and females between mating and postmating seasons, and we compared males and females within each season. We used 2 measures of movement: maximum movement (straight-line distance between 2 points) for each individual within 1 day and the proportion of all within-day movements that were > 200 m, a distance that exceeded the diameter of the postmating home ranges of most females. Within-day

movements were calculated for each case in which ± 2 locations existed for an animal within 1 day and at least 1 of the locations was not a nocturnal burrow site. Maximum movements were compared for sexes between seasons using paired Wilcoxon rank-sign tests and for seasons between sexes using Mann–Whitney U -tests. Proportions of within-day movements > 200 m were analyzed with logistic regression using generalized estimating equations (Liang and Zeger 1986), which allowed the incorporation of variation in proportions among individuals.

RESULTS

Winter rainfall and reproduction.—Rainfall totals in winter (1 October–31 March) at the study site varied greatly, ranging from only 13.7 mm in 1989–1990 to 197.8 mm in 1994–1995 (Table 1). In 3 years (1990, 1994, and 1996) we found no evidence of pregnancy, lactation, or presence of young, whereas in 1995 and 1997 all radiocollared females appeared to have produced litters. In general, low rainfall was associated with reproductive failure, but the timing of precipitation also may have been important. Although total winter rainfall preceding the 1997 active season was only slightly higher than that preceding the 1994 and 1996 seasons, all winter rainfall was received by the end of January and therefore may have been more effective in promoting germination of annual plants. In contrast, the 3 years in which squirrels failed to produce litters had had < 30 mm of rainfall by the end of January. Two of the years (1994 and 1996) had significant rainfall in February and March, yet Mohave ground squirrels did not produce litters. The 2 years in which reproduction was observed differed in total and spring rainfall, with no spring rainfall in 1997.

Postmating home ranges of females.—Size of postmating home ranges varied considerably among years for adult females (Fig. 1). The 3 females captured in 1995 were individuals that were also captured in other years, and 3 of the 4 largest home ranges in 1997 corresponded to individuals that were captured in other years. To ensure independence of observations, we restricted our analysis to 1990, 1994, and 1996, all of which were drought years with no reproduction. Size of home ranges differed among drought years for adult female MCP ($H = 13.29$, $d.f. = 2$, $P < 0.01$) and adaptive kernels ($H = 12.41$, $d.f. = 2$, $P < 0.01$) (Fig. 1). MCP in 1994 were significantly smaller ($Q = 3.61$, $P < 0.001$) than those in 1990, and 1996 MCP were also significantly smaller than those in 1990 ($Q = 2.43$, $P < 0.05$). Adaptive kernels in 1994 ($Q = 3.50$, $P < 0.001$) and in 1996 ($Q = 2.42$, $P < 0.05$) were significantly smaller than those in 1990.

Postmating home ranges of males.—Because no males were captured in 1995 and only a single male in 1994, only 3 years were available for comparison (1990, 1996, and 1997). Postmating home ranges did not differ significantly among years for MCP ($H = 4.84$, $d.f. = 3$, $P > 0.05$) or adaptive kernels ($H = 7.14$, $d.f. = 3$, $P > 0.05$). No significant differences in MCP between males and females were found during postmating seasons of 1990 ($U = 3.0$, $P > 0.05$) or 1996 ($U = 9.0$, $P > 0.05$), but male postmating MCP were larger than those of females in 1997 ($U = 11.0$, $P < 0.05$). Similarly, adaptive kernels did not differ between sexes in 1990 ($U = 3.0$, $P > 0.05$)

TABLE 1.—Monthly rainfall (mm), annual winter rainfall totals, and occurrence of reproduction for the Mohave ground squirrel, Coso Range, Inyo County, California. Years in which no evidence of pregnancy, lactation, or weaning of litters was detected are indicated as years of no reproduction. In years for which reproduction is indicated, virtually all adult females were lactating and juveniles were produced.

	October	November	December	January	February	March	Total	Reproduction
1989–1990	6.0	0.0	4.0	3.7	0.0	0.0	13.7	No
1993–1994	0.0	8.6	1.0	0.0	26.5	26.5	59.1	No
1994–1995	1.2	4.1	9.4	135.8	7.4	39.9	197.8	Yes
1995–1996	0.0	0.0	11.8	14.9	0.0	24.8	51.5	No
1996–1997	13.6	12.2	31.0	10.0	0.0	0.0	66.8	Yes

or 1996 ($U = 12.0$, $P > 0.05$) but was different in 1997 ($U = 8.0$, $P < 0.05$).

Mating season home ranges of males and females.—Male Mohave ground squirrels had very large MCPs during the 1997 mating season (median 6.73 ha, range 4.26–40.14 ha, $n = 7$) compared to those of adult females during the same season (median 0.74 ha, range 0.29–0.93 ha, $n = 6$). Male adaptive kernels (median 12.80 ha, range 5.13–44.28 ha, $n = 7$) were also larger than those of females (median 0.95 ha, range 0.58–1.43 ha, $n = 6$). Both MCPs ($U = 42$, $P < 0.01$) and adaptive kernels ($U = 42$, $P < 0.01$) were different. MCPs for males were larger ($z = 2.37$, $n = 7$, $P < 0.05$) during the mating season than postmating season (Fig. 1c), even though the postmating period was considerably longer in duration. However, adaptive kernels in the postmating season (Fig. 1d) did not differ ($z = 1.52$, $P > 0.05$) from mating season home ranges. For females, both MCP (Fig. 1a; $z = 2.21$, $P < 0.05$) and adaptive kernel (Fig. 1b; $z = 1.99$, $P < 0.05$) home ranges were larger during the postmating season than during the mating season for the 6 individuals that were present in both seasons.

The maximum distance moved within days for males during the mating season (median 391 m, range 274–1,491 m) was greater than for the postmating season, (median 130 m, range 46–427 m; $z = 2.37$, $n = 7$, $P < 0.05$). Maximum within-day movements by females during the mating season (median 138 m, range 96–213 m) did not differ ($z = 0.314$, $n = 6$, $P > 0.5$) from postmating movements (median 205 m, range 24–371 m). Maximum within-day movements for males and females were different for the mating season ($U = 42$, $P < 0.01$) but not for the postmating season ($U = 20.0$, $P > 0.05$).

During the mating season, 40.2% of within-day movements by males ($n = 7$) were >200 m, and this proportion dropped to 13.8% during the postmating period ($\chi^2 = 6.06$, $d.f. = 1$, $P < 0.05$). Females had a much lower proportion (1.5%) of within-day movements >200 m in the mating season. Although this proportion increased to 6.1% during the postmating season, this difference was not significant ($\chi^2 = 2.11$, $d.f. = 1$, $P > 0.10$). The proportion of movements >200 m differed between males and females for the mating season ($\chi^2 = 13.51$, $d.f. = 1$, $P < 0.001$) but not for the postmating season ($\chi^2 = 0.65$, $d.f. = 1$, $P > 0.40$).

Site fidelity of female ground squirrels.—In 9 cases, representing 5 individual females, a radiocollared female from 1 year of the study was found in the subsequent year. Mean proportional overlap of home ranges across years was 0.41 ± 0.16 SD, and home ranges overlapped between years for all

possible cases. In 4 cases, the home range from 1 year was contained entirely within the home range occupied during another year. Two individuals were studied for 4 years; in both cases, portions of their home ranges were used during all 4 years.

DISCUSSION

Home-range size should reflect the balance of energy demands and resource availability. The habitat-productivity hypothesis (Harestad and Bunnell 1979) predicts that home-range size should decline with increased habitat productivity because a smaller area should meet resource needs when productivity increases. This hypothesis has been tested experimentally by food supplementation (Boutin 1990) and observationally by comparing home range in areas of different productivity. Food supplementation has led to smaller home ranges in a number of small mammals, including *Tamias townsendii* (Sullivan et al. 1983), *Microtus californicus* (Ostfeld 1986), *M. townsendii* (Taitt and Krebs 1981, 1983), *Peromyscus maniculatus* (Taitt 1981), *Sciurus carolinensis* (Kenward 1985), and *Tamiasciurus hudsonicus* (Hurly and Robertson 1987). However, Slade et al. (1997) found increased movements in *M. ochrogaster* on supplemental food areas and also found that movements of reproductive voles were greater than those of nonreproductive individuals for both sexes. These authors invoked increased intruder pressure due to increased density to explain the greater movement on supplemental food grids. Mares et al. (1976, 1982) controlled population density of *Tamias striatus*, and hence intruder pressure, during a food supplementation experiment that resulted in smaller home ranges. Observational studies have also supported the general relationship between habitat productivity and home-range size (e.g., Beier and McCullough 1990; Jones 1990; Relyea et al. 2000; Rusch and Reeder 1978). However, patchy resource distribution may lead to conflicting results. For example, McShea and Schwede (1993) found that animals might expand their home ranges to include productive oaks during mast years.

Female Mohave ground squirrels varied among years in the size of their postmating home ranges. Male home-range size did not differ from that of females in 2 drought years but was greater in a year (1997) in which reproduction occurred. Because we lacked data from 2 years (1994 and 1995) for males, we did not see significant variation among years. Variation in home-range size of postmating females was associated with variation in precipitation, which in turn is related to forage availability for these small herbivores. The pattern of variation in home-range

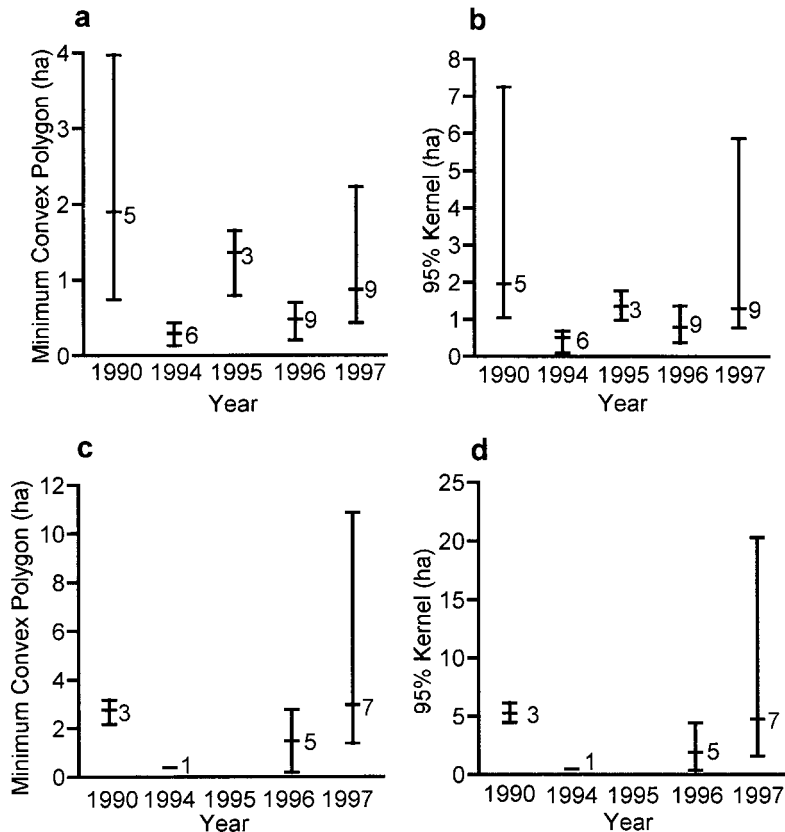


FIG. 1.—Home-range size for post-mating Mohave ground squirrels. Sizes for females are given as a) minimum convex polygons and b) 95% adaptive kernels; sizes for males as c) minimum convex polygons and d) 95% adaptive kernels. Range, median, and number of individuals are shown for each sample.

size during drought years showed an inverse relation to precipitation, as one might expect based on the habitat-productivity hypothesis. During drought years, no reproduction occurred; thus, energy demands were similar among years: female ground squirrels had to obtain sufficient food to prepare for hibernation. Home ranges in 1990 (the 2nd of 2 consecutive drought years and the year with lowest precipitation during the study) were larger than those of 1994 and 1996, the 2 years of moderate drought. The size of home ranges during drought years thus fits the pattern predicted by the habitat-productivity hypothesis: a larger home range is required to meet energy needs. A few individuals during the extreme drought year 1990 were observed making movements >200 m from nocturnal burrow locations to daily foraging areas, suggesting that they had located patches of habitat with higher food availability. Also, some individuals entered hibernation earlier in 1994 and 1996 than any of those that hibernated in 1990, suggesting that higher food availability allowed animals to prepare for hibernation at an earlier date. The contraction of home range during the years of moderate drought, in combination with the lack of reproduction, may represent a strategy of reducing energy expenditures and entering dormancy as soon as possible, a strategy also employed by other desert vertebrates (Duda et al. 1999).

Comparison of home ranges between years of moderate drought and years of higher precipitation was not possible because of a lack of independent samples. However, relatively

large home ranges were observed among 3 adult females in 1995 and 4 in 1997, years of the highest precipitation and resource availability. Reproduction occurred in both of these years, which would significantly increase the energy required by reproductive females for gestation and lactation. Energy demands for lactation in ground squirrels and other small mammals may equal or exceed the mother's own metabolic requirements (Michener 1998; Michener and McLean 1996; Millar 1978; Rickart 1982). The increase in home-range size of females from the mating season to the postmating season in 1997 suggests that the increased energy demand is associated with costs of producing a litter rather than with potential costs of mating. We hypothesize that these costs associated with reproduction should result in larger home ranges, even though habitat productivity is relatively high.

Although females exhibited considerable variation in home-range size, those that were followed for >1 year showed a high degree of site fidelity. Overlap between years was considerable, and we observed no cases of nonoverlap between any 2 home ranges, even for the 2 females that were followed for 4 years.

Behavior of males during the mating season was strikingly different from that of females. Home ranges of males in the mating season were very large, several times larger than the largest female home ranges. Large home ranges in the mating season were associated with long-distance movements. Movements within 1 day were sometimes such that a male could have traversed home ranges of several females. The proportion of

movements >200 m was much greater for males in the mating than in the postmating season, and females rarely made such movements. Although long-distance movements declined in the postmating season, males continued occasionally to make such movements early in the postmating period, resulting in large home ranges.

Increase in home-range size of males during the mating season has been reported for at least 6 other ground squirrel species (Dobson 1984). This behavior occurs in ground squirrels with territorial defense polygyny, such as *S. richardsonii* (Michener 1979, 1983) or *S. columbianus* (Murie and Harris 1978), and those with nondefense polygyny, such as *S. tereticaudus* (Dunford 1977) or *S. tridecemlineatus* (Schwagmeyer 1988). Nondefense polygyny, or scramble competition, may be favored when female density is so low that the cost of traveling between females is prohibitive or when population density is so high that the cost of defense is prohibitive (Dobson 1984). The former situation appears to apply for Mohave ground squirrels, in which female home ranges may be separated by distances >100 m and males cover large areas, making territorial defense impossible. Interactions between males or evidence of wounding by other ground squirrels were not observed during our study, an observation perhaps related to the relative scarcity of males compared to females (sex ratio of 0.27:1.0, males to females). Other anecdotal evidence supports the model of scramble competition for mates. On 1 occasion, we captured 3 different scrotal males at the burrow of a hibernating female on 3 consecutive trapping periods early in the mating season. None of these males were observed again on the study area. They may have been investigating the female's hibernation site in an attempt to mate immediately after she emerged. Male mating success is associated with mobility in *S. tridecemlineatus* (Schwagmeyer 1988), and the high degree of mobility observed in *S. mohavensis* may be associated with mate-searching behavior.

Altering size of the home range appears to be 1 mechanism by which this small herbivore adapts to an arid, variable environment. Size of female home ranges in years of no reproduction appears to vary in response to food availability. Females show a high degree of site fidelity and occupy home ranges that may be separated from one another by distances exceeding the diameter of a typical home range. Extensive male movements may be an appropriate strategy for mate searching in populations with patchy distribution and low density.

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